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Pollinators: Their Evolution, Ecology, Management, and Conservation

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Abstract

Insect pollinators are a rich and diverse group of species that have coevolved with plants to create biodiverse and productive landscapes that support ecosystem services. Bees, beetles, flies, butterflies, moths, and even ants participating in moving pollen within and between flowers, assisting the reproduction of more than 80% of all flowering plants. The value of insect pollinators to ecosystems and economies is both large and immeasurable. One of three bites of food eaten is pollinated, and countless raw materials and natural products are the result of the visitation of flowers by insects. Yet, these keystone species face survival challenges driven by habitat loss, pests, disease, pesticides, and climate change. Conservation, restoration, and management seek to build back resilience into these systems, without which our world would be unrecognizable.

Keywords: pollination, coevolution, ecosystem services, Hymenoptera, Lepidoptera, Diptera, Coleoptera, agriculture, conservation

1. Introduction

Pollination is the movement of pollen from the anther (male part) to the stigma (female part) of a flower. It is the manner in which seed plants, or *spermatophytes*, reproduce. Although this process can occur by wind or water, the dominate form in which these sessile organisms move their gametes is by animal vector. Animal pollination is a foundational ecosystem service, with an estimated 80% of flowering plants requiring or benefitting from pollination [1]. These intricate systems evolved over 140 million years ago and are the reason for the rich, diverse landscapes we enjoy and benefit from today. A diversity of animals provide pollinator services, but the majority of pollinators are insects; the most effective and important of these anthophilic insects are bees (Hymenoptera, Apoidea). These vital insects face many challenges that threaten their survival, the majority of which are the direct results of human impacts on the environment. Management in agricultural systems aims to promote bee health in order to preserve crop yields. Conservation in natural areas seeks to maintain and ensure that insect pollinator populations continue to support our ecosystems and livelihoods.

2. Evolution of pollination

2.1 Origins and the fossil record

Animal-mediated pollination evolved some 140 million years ago, when plants developed floral rewards in the form of nectar and pollen, along with attractive floral displays. Flowers evolved to attract animal visitors that would then spread pollen, in a targeted way, from one flower to another. The earliest pollinators were *palytivores*, feeding on pollen, and in the process of visiting flowers for food, got contaminated with pollen grains, moving them from one flower to the next. Beetles are seen emerging in the fossil record in the Jurassic, before the emergence of flowers, and are considered to be the first pollinators. Fossil records document beetle pollination in the Cretaceous, with the earliest record of pollen on beetles seen in amber-preserved *Cretoparacucujus cycadophilus* carrying cycad pollen dated at 100 million years old [2]. Present-day beetle pollination systems of magnolias resemble these early origins. In the discussion of the earliest pollinators there is fossil evidence from Spain that shows thrips (Thysanoptera) preserved in amber that are covered in grains of *Cycadopites* pollen [3], suggesting a diversity of prehistoric insects had associations with flowers.

Bees evolved somewhere between 140 to 70 million years ago from wasps that switched their feeding habits from a carnivorous diet of mostly other insects to pollen and nectar. The oldest fossil record of bees is a specimen of stingless bee, *Trigona prisca*, found in the United States that is dated to between 96 and 74 million years old, from the Upper Cretaceous [4]. Fossil records of *Apis* bees have been found in Western Germany that date to the Lower Miocene (approximately 25 million years ago). These are considered to be precursors to the modern day honey bee, *Apis mellifera*, arguably the most important insect pollinator. Flies appear in the fossil record about 200 million years ago; moths and butterflies are markedly older, appearing as early as 400 million years ago.

2.2 Coevolution

The coevolution of plants and insect pollinators has resulted in mutualisms that are an incredible diversification of forms and functions as plants developed ways to ensure visitation, fidelity, and pollen transfer to secure their reproduction. From the plant's perspective, attracting a visitor that will coincidentally get covered in pollen before visiting another food source was the first step in the development of tailored systems that allowed plants to produce fewer pollen grains. Flowers evolved as specialized structures to further attract insect visitors. This included elaborate shapes, scents, and colours. Scents and colours advertise flowers to pollinators looking for food in new landscapes.

The size and shape of the flower facilitates the transfer of pollen to the pollinator, with adaptations to each group. Complicated morphologies that squeeze, and in some cases trap, pollinators work to increase the chance of transferring pollen. Orchids are famous for specialized pollination systems, including trap pollination, as exhibited by *Cypripedium* species. Orchid bees attempting to visit Lady's Slippers flowers slip into a chamber where they are trapped temporarily, and presented with a single, narrow opening through which to exit. As they squeeze through this narrow opening they move past the sticky *pollinia* (large pollen sacks) that are deposited on their backs. Another group of flowers with trap blossoms are the *Arums*. These plants trap pollinating flies within their base where the anthers are found until the pollen is mature, opening to release pollen-covered flies and beetles that will then go and visit other flowers. Many trap-flowers use deception to attract

insect visitors, mimicking reproductive pheromones or the scent of food sources (i.e., carrion). Another form of deceptive pollination used by some flowers, such as orchids, is Pouyannian mimicry: tricking a male visitor into thinking there is a receptive mate. The mirror orchid, *Ophrys speculum*, appears in colour and shape like the female scoliid wasp (Scoliidae), this tricks the male into attempting to mate, referred to as *pseudocopulation*, which then triggers the release of pollen onto the unsuspecting insect.

Concurrently insects evolved individualized morphologies and behaviours to increase their fitness and optimize their ability to capitalize on floral resources. Insects are likely pollen vectors, often possessing hairs or scales that pollen attaches to easily. Bees, the most effective and efficient pollinators, have branched hairs that often occur in dense aggregations called *scopa* that are specialized to carry pollen. Unlike other pollinators that visit flowers to feed on nectar and pollen, accidentally getting contaminated with pollen, bees actively collect pollen to provision for their offspring. Early bees collected pollen in their digestive systems, holding it in their *crop*. Some more primitive bees in the family Colletidae still make use of ingesting pollen as they do not have the pollen-carrying hairs on their body. Most bees, however, carry pollen in an external load, which can also be used as an identifying characteristic.

3. Pollination systems

Over the last 120 million years, pollinators have diversified an incredible amount. Bees, butterflies, moths, flies, beetles, and wasps have evolved to fill specific niches in the environment. The generalized characteristics of plant-pollinator systems are commonly described in pollination syndromes; predictive sets of plant morphology and phenology that align with the preferences of pollinators. Insect pollinator syndromes include bee and wasp pollination (melittophily); butterfly pollination (psychophily); moth pollination (phalaenophily); fly pollination (myophily and sapromyophily); beetle pollination (cantharophily); and even ant pollination (myrmecophily) (**Table 1**). Using the theory of pollination syndromes, Charles Darwin postulated that the pale and fragrant Christmas Orchid, *Angraecum sesquipedale*, was likely pollinated by a moth with a proboscis equal in length to the long nectary possessed by this flower, measuring more than 25 cm in some cases. Darwin passed away before he ever validated his prediction, but two decades later a sphinx moth, *Xanthopan morganii*, with an impressive 30 cm proboscis was found to in fact be a visitor of the orchid.

3.1 Pollinator syndromes

3.1.1 Canatharophily

Beetle pollination: With more than 380,000 species of beetles globally it is assumed that more than 90% of all pollinated plants have associations with beetles. Beetles may not be the primary pollinator, but their ubiquitous presence makes them important anthophiles. Flowers that are pollinated by beetles, or those that present characteristics to attract beetles, are commonly large; pale white, cream or green in colour; and have a heavy scent that is sometimes foul, mimicking carrion. Beetle bodies are robust and they are often clumsy, correspondingly beetle-pollinated flowers are often flat or disc-shaped. The pollen is easily accessible as beetles have minimal ability to handle and manipulate it. Beetles have been called destructive pollinators, visiting flowers to feed on floral

Floral Trait	Colour	Shape	Nectar Guides	Odour	Pollen	Nectar	Bloom
Canatharophily (beetle)	pale/dull, white, green	large, bowl-shaped	none	strong fruity or foul	abundant	accessible nectaries	day
Melittophily (bees, pollen wasps)	yellow, blue, purple, ultraviolet	complex, disc, or tubular	present, obvious	fragrant, pleasant	abundant	abundant	day
Psychophily (butterflies)	red, pink, purple, bright	disc shaped, landing pad	present	strong and fragrant	limited	abundant, deep	day
Phalaenophily (moths)	pale, cream, white, yellow	tubular, with and without landing pad	none	strong and fragrant	limited	abundant, deep	day and night
Myophily (flies)	yellow, white	disc shaped	present	strong and fragrant	limited	abundant	day and night
Sapromyophily (carrion flies)	marron, green, dull	funnel or trap, small	none	strong and putrid	limited	absent	day and night
Myrmacophily (ants)	varied	open, small	none	none	varied	abundant, extra-floral nectaries	day

Table 1.
Insect Pollinator Syndromes, various floral characteristics that correspond to generalized preferences and use patterns of seven types of insect visitors.

parts, or the pollen directly. For this reason, many beetle-pollinated plants have extra protective structures around their ovaries. Pollen is the dominant reward produced by beetle-pollinated flowers.

3.1.2 *Melittophily*

Bee pollination: Flowers that are visited by bees have perhaps the greatest diversity in form. Bees often make use of open, disc-shape flowers, but are also able to access more complicated floral forms, even those that require complicated floral handling. For example, flowers in the pea family (Fabaceae) have a complex, asymmetrical morphology, with a keel petal that covers the opening and access to nectar and pollen. Both strength and persistence are required to access the floral rewards in such blossoms. Bee-pollinated flowers are commonly yellow, blue, or purple.

(**Figure 1**). They also commonly possess ultraviolet colouration as bees can see this part of the light spectrum. Many bee-pollinated flowers have nectar guides, areas of colour that highlight the location where they nectaries are located. Nectar guides focus pollinator effort and optimize pollination. Bee-pollinated flowers are heavily scented, allowing an additional chemical sensory way for bees to locate them. Although melittophily predominantly refers to bees, pollen wasps are attracted to



Figure 1.
Small sweat bee (Halictus sp.) visiting a compound, disc-shaped, purple flower (Asteraceae) representative of melittophily. [photo credit: Amber Barnes].

the same set of morphological characteristics. Bees are specifically adapted to be the ideal pollinators. While most pollinating insects visit flowers to feed on nectar, accidentally getting covered in pollen, bees purposely collect pollen to feed their young. Nectar is a food source for adult bees, and this high-energy carbohydrate food powers their metabolically expensive flight. For this reason, bee-pollinated flowers provide abundant nectar and pollen.

3.1.3 Psychophily

Butterfly pollination: Flowers pollinated by butterflies are commonly disc-shaped or compound in structure to provide an easy landing pad. Members of the family Asteraceae are widely visited by butterflies. Butterfly-pollinated flowers are obvious and showy, usually pink, red, or purple, and they are highly scented. Unlike bees, butterflies can see the colour red, and correspondingly many of the flowers visited by butterflies are red. Butterflies feed on nectar using a proboscis and are looking for abundant nectar. Nectaries can be located in tubes or spurs that are accessible by this long proboscis. The anthers of butterfly-pollinated flowers are

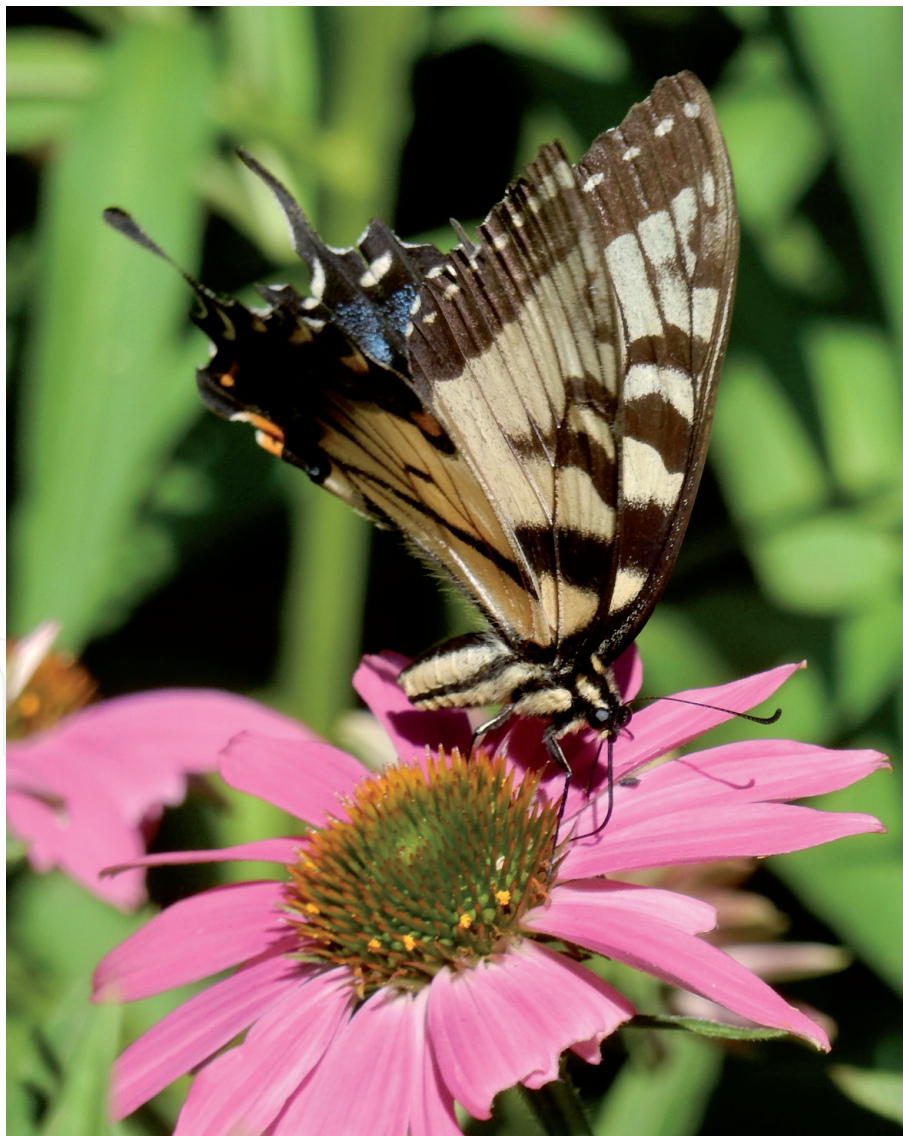


Figure 2. An Eastern Tiger Swallowtail butterfly (*Papilio glaucus*) feeding on a pink flower (Asteraceae) with a large disc-shaped landing pad representative of psychophily. [photo credit: Amber Barnes].

usually located in places that would deposit pollen on the heads or undersides of butterflies. It is common for butterflies to land on compound flowers and proceed to feed at multiple sites. (**Figure 2**). Butterflies are sun-seekers that exhibit basking behaviours, enjoying flat flowers in sunny locations. A common group of specialized butterfly-pollinated plants are the milkweeds (family Apocynaceae, genus *Asclepias*). The flowers of these plants present the characteristics of psychophily: they are colourful, clustered, and tubular. Additionally, monarch butterflies, *Dannus plexippus*, are co-evolved with *Asclepias* species; the caterpillars are able to eat their toxic foliage, which contains cardenolides, resulting in the development a chemical defense against predators. (**Figures 3-6**).

3.1.4 Phalaenophily

Moth pollination: Flowers pollinated by moths share some characteristics with butterfly-pollinated flowers, including nectaries in deep spurs and attractive scents. Most moths are active in the evening, or at dawn and dusk (crepuscular), so their flowers are generally less colourful and more perfumed. Moth-pollinated flowers



Figure 3.
Monarch (*Dannus plexippus*) egg laid on the underside of a milkweed (*Asclepias*) leaf. [photo credit: Amber Barnes].



Figure 4. Monarch (*Danus plexippus*) caterpillar feeding on milkweed (*Asclepias*); this behaviour instills a chemical defense in the caterpillar and butterfly. [photo credit: Amber Barnes].

tend to be white or cream coloured. The amount of nectar produced is relatively high as many moths hover while they access their food and have a high metabolic demand.

3.1.5 Myophily

Fly pollination: Pollinating flies that feed on nectar are attracted to a similar variety of floral types as bees are attracted to. Fly-pollinated flowers tend to display a diversity of colours and shapes, although they tend not to be as complex as those visited by bees. The scent emitted by these flowers is also usually quite fragrant and potent to aid flies in locating the flowers. Flies are nectar feeders, and fly pollinated flowers provide ample nectar.

3.1.6 Sapromyophily

Fly pollination by carrion or dung seekers: Less common than myophily, flowers pollinated by flies seeking animal flesh or dung as egg-laying substrates mimic these elements. They are heavily scented to mimic foul odours. The flowers can be small, colourless, or a dull purple/pink, with a sticky secretion. Trap-blossoms are



Figure 5.
Monarch (Danus plexippus) chrysalis. [photo credit: Amber Barnes].

also common. These flowers do not offer rewards; instead they trick the insect into visitation. A wonderful example of sapromyophily is the giant corpse plant, or titan arum, *Amorphophallus titanum*. The gigantic flower produced by this arum can be upwards of 2 meters tall, and produces a strong, foul odour that resembles rotting flesh. Flesh flies and carrion beetles are attracted to this plant; as they attempt to find a meal or lay eggs they are trapped inside the giant flower until it wilts, releasing them after they have been covered in pollen.

3.1.7 Myrmecophily

Ant pollination: Ants are minor pollinators, and are not attracted to showy floral structures. In many cases the flowers of ant pollinated plants are small, often occurring in clumps. The flowers can be also located at the base of stems. The plants themselves are low-growing and accessible from the ground. Ants feed on nectar found inside of the flowers as well as on extra-floral nectaries. Ant-pollinated plants occur in arid or alpine environments. Examples of ant-pollinated plants include Small's stonecrop (*Diamorpha smallii*), alpine nailwort (*Paronychia pulvinata*), and Cascade knotweed (*Polygonum cascadenae*), as well as two alpine orchid species, *Chamorchis alpine* and *Dactylorhiza viridis*.



Figure 6.
Adult monarch butterfly (Danaus plexippus) feeding on the flowers of common milkweed (Asclepias speciosa).
[photo credit: Amber Barnes].

3.2 Adaptations for pollination and flower visitation

3.2.1 Physical adaptations

Each arthropod pollinator group has a specific physical adaptation for accessing pollen and nectar. Most insects adapted to pollen collection are covered in hairs or scales. Bees are the most highly adapted to collecting and carrying pollen. Their bodies are covered in dense, bifurcated hairs that grab onto pollen. Many bees have dense aggregations of pollen-carrying hairs, called scopa, on their hind legs or the underside of their abdomen. The placement of pollen-carrying hairs can aid in general identification of bees. Members of the family Megachilidae (*Megachile*, *Osmia*, *Anthidium*, *Hoplitis*, and *Chalicodoma*), commonly known as leafcutter bees, mason bees, and carder bees, are all identifiable by their ventral abdominal scopa. Bees in the family Andrenidae carry pollen on the upper portion of their hind legs, while members of the family Halictidae carry pollen down the length of their hind legs. Members of the family Apidae also carry pollen on their hind legs, but generally in a more compacted pattern; some have further specialized

structures called *corbicula* where they can carry a tightly packed ball (**Figure 7**); this is common in honey bees (*Apis mellifera*), bumble bees (*Bombus* spp.), and carpenter bees (*Xylocopa* spp.).

The adaptations of other insect pollinators are specific to accessing nectar and pollen for food. Flies do not actively collect pollen, but are effective pollinators because they are covered in hair. Flies feed on nectar and access it through the use of a shortened set of sucking mouth parts. Nectar taken in this manner has to be shallow and accessible. Butterflies and moths are covered in scales, not only on their wings, but also on their face, thorax, abdomen, and even their legs. Pollen is transferred to these scales when they feed, and then transferred to another flower when they make another visit. Butterflies and moths feed on nectar accessed through a proboscis, which in some cases is extremely long in order to access nectar in deep nectaries. Beetles feed on pollen, collecting it with their mouthparts. Some have additional adaptations such as rows of dense hairs on their maxilla or labium, which act as a pollen broom that helps convey pollen into their mouth.

Pollen and nectar are the dominant rewards sought by anthophiles, but some also collect various oils, resins, and other substances. Bees in the genera *Eulema*



Figure 7.
A bumble bee (*Bombus* sp.) carrying a large, round load of pollen held on the corbicula. [photo credit: Amber Barnes].

have very dense hairs on their hind legs that hold oils. The males of some species of *Euglossa* have specialized structures on their hind tibia called perfume pouches where they collect floral scents that they then use to attract females. Honey bees and stingless bees collect plant resins, oils, and other secretions that they then mix with their saliva and nectar to make propolis.

3.2.2 Behaviours that optimize pollen collection

Feeding habits vary greatly between insect pollinators, and even within genera, and species of each group. Some species exhibit specialization for one host plant species and are considered monoleptic. Others forage on multiple species within one plant genus, a feeding habit that is termed oligolectic. A broader repertoire for multiple species in similar plant genera is called mesolectic. Some have a much broader repertoire and visit multiple species within multiple genera families and are considered polylectic to various degrees [5]. Honey bees, which are considered broadly polylectic or generalist feeders, forage on a wide spectrum of food resources within a landscape. One-to-one specialized relationships where there is a single pollinator for a single plant, though interesting and highlight specialized, are rare. Research into pollination networks within ecosystems has shown that overlap and redundancy are much more common. Bipartite pollinator networks are useful tools to understanding how pollinators and plants within an ecosystem interact, building resilience and buffering against change (Figure 8) [6–8].

Some pollinators have specific behaviours they use to increase pollen collection. In some cases the coevolution of this mutualism has resulted in plants that are so specialized they can only be effectively pollinated by certain pollinators. Buzz pollination, or *sonication*, is one such system. In sonication, a pollinator holds on to a flower and vibrates its wings to release pollen. Bumble bees and other large-bodied

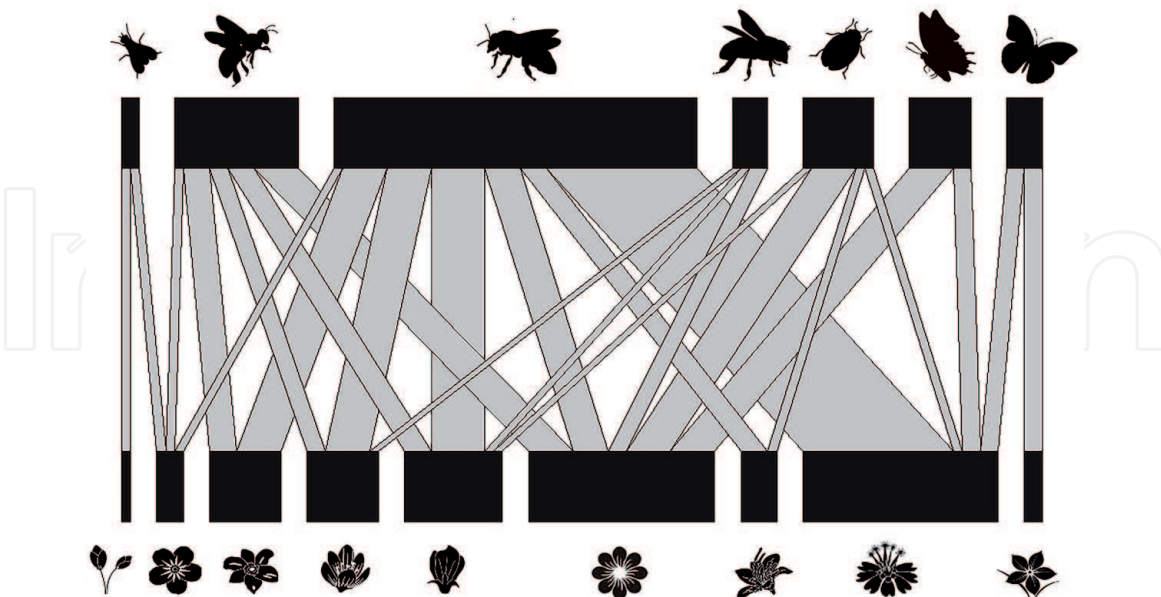


Figure 8.

A representative bipartite network visualizing the linkages and connections in a plant-pollinator system. Linkages between plants and pollinators are indicated with connecting lines, line width represents the relative dominance of the linkage in the system. Bands below pollinators represent relative dominance of each taxon in the system. Similarly, bands above the flowers represent the relative dominance in terms of usage by pollinators in the system. Using these networks allows for keystone species and resilience levels in the pollination systems to be determined, and can also identify plants and pollinators that may be more at risk. [figure credit Victoria Wojcik].

insect pollinators are prime examples. Plants in the family Solanacea (nightshades), which includes tomatoes, eggplants, and potatoes, have adapted to buzz pollination; their anthers are enclosed in a structure and pollen can only be released through vibration.

Bees present the most refined versions of behavioural adaptations to optimize pollen and nectar collection. Flight is metabolically expensive, yet it is the dominant manner in which most insect pollinators find and access their food. Patterns in how pollinators work within and between flowers show both energy optimization through shortened flight patterns and minimizing efforts against gravity, as well as ways to increase the chance of finding nectar. Though they often search for sites of forage, bees are central-place foragers, meaning they tend to forage on food resources nearer to their nest site. For colonial species like honey bees and bumble bees, this means foraging near to their nest. For solitary species this means nesting near abundant food resources. Colonial species with an established nest in a dearth of resources will relocate.

When bees are foraging in a field, they focus the attention of an individual foraging trip on the same species of flower, even if they feed on a diversity of sources. Flight patterns are impacted by resource abundance as an adaptation to optimizing rewards. When flying through a resource-rich floral field they have been documented to make more turns in their flight, stopping more often to feed. In fields with less abundant resources, they fly straight more often, searching for abundant, localized forage. Bees that feed on a wide range of flowers also focus their foraging efforts on the most dominant species in the landscape, a strategy that targets rewards and balances energy expenditure. Optimizing forage to what is in bloom and providing the most nectar and pollen that day minimizes the flight time between nest and flowers and conserves energy. Energy optimization is used for resource seeking and floral selection. Bees tend to use complex floral resources that have vertical structure from the top down, again conserving energy by minimizing the needs to fly against gravity. This is most evident in tropical systems where bees are foraging on flowering trees.

The culmination of behavioural adaptations to optimize foraging is social communication and recruitment foraging exhibited by social bees, such as honey bees, stingless bees, and bumble bees. Bumble bees exhibit rudimentary communication through movement and wing vibrations that appear to signal that the arriving forager has visited profitable food resources. Honey bees and stingless bees have a complicated dance language, commonly called the waggle dance in honey bees. Through this dance they communicate the quality and location of food resources. Honey bees provide information on distance and direction, while stingless bees also provide information about the vertical plane in which food is found as many stingless bees forage in forest ecosystems.

4. Globally pollinator diversity

Globally there are estimated to be more than 1,000,000 species of insect pollinators. This includes nearly 800,000 beetles that are not likely to be the main pollinator of most plants, but are the dominant anthophiles.

Speaking to the most effective and functional pollinators, there are currently some 20,000 species of bees known globally. This diversity is represented by seven families: Andrenidae, the mining bees; Apidae, honey bees, carpenter bee, stingless bees, long-horned bees, and orchid bees; Colletidae, the plaster or cellophane bees; Halictidae, the sweat bees; Megachilidae, the leaf-cutter and mason

bees; Mellittidae, the oil collecting bees, and Stenotritidae, the fast flying bees. Stenotritidae are only found in Australia; the other families are present across the globe.

Pollinating wasps include members of the subfamily Masarinae, which have a visual resemblance to vespid wasps. Fig wasps, members of the family Agaonidae, are a diverse group of more than 900 species of tiny wasps that have a unique specialized pollination system with figs (genus *Ficus*). Fig flowers have evolved an internalized structure that is accessible through a small opening. Female fig wasps covered in pollen enter the fig flower to lay their eggs inside, transferring the pollen of the fig that they have hatched from. The eggs of the fig wasp mature and hatch inside of the fig flower. Male and female offspring mate with each other, the males remain in the flower, and the females exit the flower to start the cycle over again.

There are some 150,000 species of moths and 17,000 species of butterflies globally. Many of the relationships that butterflies have with flowers are more specialized, particularly those that include access to nectar in deep nectaries. Both butterflies and moths require host plants for their caterpillar development, in many cases the same plants that provide nectar to adults also serve as larval host plants (**Figures 3-6**).

Though there are roughly 160,000 fly species globally, a narrow spectrum of these species are pollinating anthophiles. The most common group of pollinating flies is the family Syrphidae, with nearly 6000 species. Syrphid flies, also known as flower flies, often resemble bees and mimic these species. Other pollinating flies include midges, such as members of the genus *Forcipomyia*, which pollinate cacao flowers, and mosquitoes, including the snowpol mosquito *Aedes communis* that pollinates the blunt-leaf orchid *Platanthera obtusata*.

Pollinating insects are present in all terrestrial ecosystems, with the exception of Antarctica. Patterns of diversity include both ecosystem types and geographic regions that have higher richness than others. Arid landscapes tend to have higher pollinator species richness, and though this might seem counter intuitive, these ecosystems are characterized by distinct seasonal patterns, often with short precipitation windows, and environmental extremes. This multitude of temporal niches has driven a diversity of pollinator mutualisms. For some species, such as bees, there are distinct bimodal patterns of richness, with far northern and far southern latitudes having less richness than mid-latitudes. In the case of bees, their niche is often filled by flies closer to the poles. This same pattern of declining richness and substitution of flies into bee niches is seen in alpine ecosystems as elevation increases. Meadow and prairie ecosystems are generally considered to be hot-spots of insect pollinator diversity, owing to the richness of flowers and open space. Conversely, temperate forest systems have previously been considered to be lower in pollinator richness, but recent evidence suggests that these systems are in fact abundant with species.

5. Nesting and other habitat needs

Pollinating insects have a diversity of nesting strategies and habitat needs for reproduction. Bees are famous for constructing nests; for social species this including building hives and constructing combs and brood chambers for their young. Honey bees, stingless bees, and bumble bees all produce wax which they use to build nest cells. Solitary bees have a more varied set of nesting strategies. The majority excavate nesting in the soil, creating chambers for brood.

Some species make use of preexisting holes, lining them with various materials. Leafcutter bees cut and fold leaves to make nest cells. Mason bees collect mud to form their nests. Some bees excavate nests in the pith of plant stems, and some, like carpenter bees, are able to chew into wood. Solitary bees provision for their offspring, laying an egg that hatches, eats a pollen store, pupates, and then emerges as an adult.

Butterflies and moths lay eggs on host plants, their young emerge and eat the plant materials, eventually pupating, and emerging as adults. Pollinating flies lay their eggs in leaf litter or other substrates. Beetles have varied nesting lifestyles, including leaf litter and burrowing.

6. Agriculture and food production

Pollinators are responsible for one of every three bites of food we eat [9, 10]. This corresponds to an enormous economic contribution that has been estimated recently to be upwards of 153 billion US dollars annually [11]. Corn, wheat, and rice – the carbohydrate staples of most cultural diets – are wind pollinated, but nearly 80% of the crops that are cultivated across the globe require or benefit from pollinators [10]. Pollinated foods provide the necessary and essential nutrients for the human diet, including foods high in antioxidants, as well as vitamins A, B, and C [12].

The major insect pollinators of agricultural crops are bees and flies, with other insect pollinators generally considered to play minimal roles in crop production. There are many crops, fruits, and spices that are pollinated by moths, wasps, and even beetles, especially in more tropical parts of the world. Butterflies, however, are not known to pollinate any crops.

Honey bees are famous in agriculture because they can be managed and moved between crops to pollinate what is in bloom. As generalist pollinators, honey bees will visit most crops, but they are not universally the ideal pollinator for each crop. Bumble bees are ideal pollinators for tomatoes, eggplants, and peppers as these crops require sonication, or buzz pollination. Squash bees, *Peponapis* spp., pollinate pumpkins, squash, melons, and zucchinis [13]. Orchard and mason bees (*Osmia* spp.) are ideal pollinators of stone fruit (cherries, almonds, etc.), apples, and pears [13]. In the case of pears they outperform honey bees who find pear nectar too low in sugar for their taste. Leafcutter bees (*Megachile* spp.) are good pollinators of alfalfa and other legumes [13]. Vanilla orchids are pollinated by orchid bees in the genera *Euglossa* and *Eulema*.

Flies play key pollination roles in many crops, including staples such as cocoa (midges in the genera *Ceratopogonidae*, *Forcipomyia*, and *Euprojoannisia*), coffee, and tea [13]. Mangos, kolanut, lychee, coconut, nutmeg, acerola, and avocados are pollinated by flies. Flies also pollinate many common field crops such as carrots, onions, leek, parsnip, and dill [13]. Moths have roles in pollinating crops including yucca, neem, papaya, passionfruit, and nutmeg [13]. Wasps are known for pollinating figs, but also play roles in pollinating kenaf, lychee, and cotton [13]. Beetles pollinate pomegranates, parsnip, and nutmeg [13].

7. Additional ecosystem services supported by insect pollinators

Food production and the reproduction of wild plants are considered critical provisional ecosystem services, without which the Earth could not exist in its

life-supporting state. It has already been established that insect pollinators are critical to food production and plant reproduction [14]. Additionally, insect pollinators are keystone in provisional, regulating, and cultural ecosystem services.

Hardwood products, fibers, textiles, dyes, scents, plant derived chemicals, and pharmaceutical products are the products of flowering plants that require pollination [15, 16]. Insect pollinators also have a role in maintaining reproduction in plants that fix and cycle nitrogen, such as legumes [17]. Some of the very behaviours and lifestyles of these insects, such as ground nesting, promote soil aeration and nutrient cycling. About 60% of bee species nest in the ground, and this behaviour provides soil disruption [18]. Vegetation that defines ecosystems, and buffers the impacts of severe weather and erosion is again commonly insect-pollinated. The California chaparral ecosystem is one example. Plant species responsible for soil stabilization along hillsides require pollinators for reproduction [19]. A lack of pollinators and the eventual senescence of these species can cause vulnerability to landslides during annual wet periods. Similarly, coastal mangrove communities that provide protection during storm events need pollinators for reproduction [20, 21]. Tropical forest communities, which play significant roles in carbon sequestration, are dominated by pollinator-dependent species, with an estimate of nearly 95% dependence [1].

Cultural inspiration and spiritual enrichment is provided by ecosystems that depend on insect pollinators, as well as the pollinators themselves. Mayan artwork depicts the practice of *meliponiculture*, and this honey was used in sacred rituals and as food. There are multiple references to honey in Eastern and Western religious texts and rituals. The cleansing and rebirthing properties of honey are mentioned heavily in Jewish text and honey is used in celebration of the New Year. In Hinduism honey, *madhu*, is as one of the five sacred elixirs of immortality. In Buddhism honey is given as a gift of honour to monks. Contemporary art and culture also features insect pollinators heavily, be it depictions of bees as mascots for breakfast cereal or our fascination with the metamorphosis of caterpillars into butterflies.

7.1 Managing insect pollination services

7.1.1 Beekeeping

With the significant role that managed honey bees play in global food production their health and wellbeing a key concern for beekeepers, farmers, and governments. Today, honey bees are managed by beekeepers to maintain high quality colonies that meet minimum pollination contract requirements or that produce marketable amounts of quality honey for commercial markets. A conservative estimate of the history of beekeeping dates the practice at 5000–6000 BCE, with images on African pottery and Egyptian artifacts depicting the practice. Modern day beekeeping, the management of honey bees in hives with mobile combs, began in 18th century Europe. In the Americas, the Mayans practiced *meliponiculture*, keeping stingless bees in the genus *Melipona* for honey that was used in rituals and as a sacred food.

7.1.2 Other managed bees

Other managed bees include multiple species of bumble bees, which can be reared in boxed colonies and used in greenhouse and field pollination. A handful

of solitary bees are also reared for commercial use. The alfalfa leafcutting bee, *Megachile rotundata*, is reared in tube nests and used to pollinate alfalfa. Orchard bees such as the blue orchard bee, *Osmia lignaria*, and the red mason bee *Osmia bicornis*, are managed in North America and Europe, respectively, for orchard pollination. The alkali bee, *Nomia melanderi*, is a ground nesting sweat bee that prefers alkali soils. This species also pollinates alfalfa and is commercially managed either in movable binds of soil containing nest cells, or by seeding areas near farms with nests as this species recolonizes its home range.

7.1.3 Other managed insect pollinators

Many other insect pollinators and other bees are managed by providing nesting and feeding opportunities near to crops of interest. The establishment of floral resource strips near agricultural increases the occurrence of many species of solitary bees, as well as other insect pollinators such as flies, butterflies, and moths. In the case of some fly pollinators, such as those that pollinate cocoa, leaving leaf litter in plantations encourages nesting opportunities and is thought to boost populations and pollination.

8. Threats and challenges

Insect pollinators face survival challenges that stem from multiple, interacting factors. Habitat loss; pests and disease; invasive species; pesticides; and climate change all make survival more difficult for these essential species. These factors work both independently and in synergy to undermine the survival of insect pollinators, and the people and plants that depend on them.

8.1 Habitat decline

The primary threat to insect pollinators is habitat decline, both in terms of the available area, and in the richness of plant species available to feed on. Agricultural intensification, increased urbanization, and the extractive industry disturbs and removes habitat resources. Habitat loss reduces feeding opportunities by both reducing the amount and variety of food sources, and also reduces opportunities for nesting. When habitat loss increases fragmentation reproductive consequences can also occur, include narrowing genetics and reproductive isolation for both pollinators and plants [22].

8.2 Pests and disease

Pests and disease challenge the survival of pollinators, and have increased in their impacts as international travel, commerce, and industrialized agriculture provide increased opportunities for spread. So much of our agricultural productivity is dependent on the honey bee (*Apis mellifera*) that it is no wonder that our attention is drawn to their plight. Honey bees and other bees are subjected to pests and parasites, such as *Varroa destructor*, an external mite that weakens bees by feeding off of their hemolymph. Common diseases include *Nosema ceranae*, a fungal infection that impacts digestion and the absorption of nutrients and foul brood (American foul brood: *Paenibacillus larvae* and European foul brood: *Melissococcus plutonius*), which infect larvae causes mortality. A slate of viruses also infects bees, including deformed wing virus, which causes body malformations; and sacbrood virus, which

causes mortality before pupation. These bee diseases have been identified from honey bees, but are known to spread to wild populations of bumble bees and other species, presenting a conservation challenge and further stressor in these unmanaged species.

8.3 Pesticides

Pesticides and other chemical pollutants threaten insect pollinators, in some cases causing direct mortality, and in others causing significant sublethal impacts that reduce pollinator function, cognition, and reproduction. The vast majority of targeted pests are insects, and correspondingly beneficial insects within these systems suffer. Most pollinator poisoning occurs when pollinator toxic pesticides are applied to crops during the blooming period. Poisoning of pollinators can also result from drift onto adjoining crops or plants, the contamination of drinking water, and the uptake of systemic pesticides that move through the soil by non-target plant species.

8.4 Invasive species

Invasive species, both plants and other insect pollinators, can alter local ecosystems, in some cases causing significant enough change that pollination webs are modified and individual mutualisms are impacted. Invasive plant species with aggressive, generalist growth patterns can become the dominant species in a landscape. This transition in landscape composition can mean rare resources of more specialized pollinators dwindle. The basic foraging biology of pollinators can also promote the establishment and spread of invasive plants. As generalist pollinators preferentially visit the most dominant species in a landscape, this can provide a feedback loop that exacerbates the issue. Non-native plant species that have not coevolved with the native pollinator fauna may present other challenges such as a phenological mismatch, floral morphology that is difficult to access, and variability in both pollen protein and amino acids and nectar sugar concentration.

Dietary variability can impact growth and reproduction in species that have coevolved with certain food profiles. Invasive arthropod pollinators have also been noted to cause stress on plant-pollinator systems, including competitive interactions with native species that could result in extirpation or extinction, or the transmission of new pathogens and diseases. There are multiple examples of non-native bees that have established outside of their range; they are commonly tube nesters that have been accidentally introduced. One such example is *Megachile sculpturalis*, commonly known as the giant resin bee, this species is aggressive and has been shown to evict other *Megachile* species from their nests, and even has been aggressive towards carpenter bees (*Xylocopa* spp.). Purposeful introductions for agriculture have occurred as well, including two Asian species, *Osmia cornifrons* and *Pithitis smaragula*, which were introduced to the United States.

8.5 Climate change

Climate change is a looming threat, impacting both insect pollinators directly, and changing the floral ecosystems these species depend on. Changes in richness and diversity; range changes and restrictions; changes in flight periods; as well as asynchrony between coevolved pollinators and plants are the primary concerns as the climate changes. As patterns of precipitation and temperatures change the

range of conditions that define an appropriate niche for insect pollinators and their plants can change.

Overall patterns of pollinator richness have been predicted to change, which includes both increase and decreases in regional richness. For example, predictive modelling of butterfly richness in Canada in a climate change scenario showed decreases at the most northern and southern latitudes, but increase in richness at mid-latitudes [23]. In some cases this will be a range contraction, and in some more severe cases extirpations and extinctions as species are pushed to the extremes for their biology and phenotypic plasticity. Historical museum records of bumble bee occurrence compared to current occurrence data showed a dramatic range restriction in United States [24].

The cues that trigger plant phenology, such as bloom and bud drop, are largely dependent on photoperiod, which remains constant as temperatures change. The maturation and development of insects is largely driven by temperature, with most species requiring a specific number of degree days to pupate and emerge as adults. The development of asynchrony between bloom and the emergence of insect pollinators is another threat; recent studies from Europe indicate that on average there been a two-day dissociation between plants and their pollinators in the past 30 years [25], with some pairings showing as much as 10 days, as is the case between blackcurrant and *Osmia rufa*. Ten days may appear extreme, but a 2011 study of pollinator phenology in the United States found that on average bees are emerging 10 days earlier in the calendar year when compare to historical records from a century ago [26].

9. Conservation actions

Pollinator populations are changing in response to a changing world. The previously mentioned list of threats and challenges has resulted in many insect pollinators being in decline, with many species listed as threatened or endangered. Extinctions in pollinator species have also occurred. When pollinators decline, the plants that they depend on, the productivity of ecosystems, and the services they provide parallel this trend [27]. Conservation actions that aim to support arthropod pollinators include policy frameworks that protect natural areas, moving towards sustainable agricultural systems that include increasing non-crop forage, active programs to protect and boost populations of listed species, policy that works to reduce stressors such as pesticides, and climate positive actions. Key efforts seek to raise awareness of the essential roles that the small, often overlooked and misunderstood, species play in supporting our daily lives.

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